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Nest Defense and Conspecific Enemy Recognition in the Desert Ant *Cataglyphis fortis*

Markus Knaden¹ and Rüdiger Wehner^{1,2}

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*This study focuses on different factors affecting the level of aggression in the desert ant *Cataglyphis fortis*. We found that the readiness to fight against conspecific ants was high in ants captured close to the nest entrance (0- and 1-m distances). At a 5-m distance from the nest entrance the level of aggression was significantly lower. As the mean foraging range in desert ants by far exceeds this distance, the present account clearly shows that in *C. fortis* aggressive behavior is displayed in the context of nest, rather than food-territory defense. In addition, ants were more aggressive against members of a colony with which they had recently exchanged aggressive encounters than against members of a yet unknown colony. This finding is discussed in terms of a learned, enemy-specific label-template recognition process.*

KEY WORDS: aggression; *Cataglyphis*; “dear-enemy” phenomenon; enemy recognition; territoriality.

INTRODUCTION

The desert ant *Cataglyphis fortis* (Wehner, 1983) is the only species of ants inhabiting the vast plains of the North African salt pans. The colonies of this medium-sized monomorphic *Cataglyphis* species (body length, 5.5–9.6 mm; head width, 1.1–2.4 mm; [Wehner, 1983; Dillier, 1998]) comprise only about 50 foragers, which search individually for dead arthropods (Wehner, 1983, 1987). Neither in this nor in any other *Cataglyphis* species studied has

¹University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

²To whom correspondence should be addressed. Fax: 0041-1-6355716. e-mail: rwehner@zool.unizh.ch.

any system of recruitment been found so far. Ultimately, this might be due to the scarce and nonpatchy food distribution within the ants' habitats, but proximately it might be due to the high surface temperatures, which prevent route marking by odor. At any one time and any one place in the ants' foraging range, members of different conspecific colonies rarely meet. At our central Tunisian study site the mean nearest neighbor distance between colonies is about 40 m (Dillier, 1998), and the mean maximum foraging distance is about 24 m (Selchow and Wehner, unpublished), but in the more food-impooverished vast salt pans of southern Tunisia, the mean foraging distance amounts to 90 m and individual *C. fortis* foragers may leave the nest for up to 200 m (Wehner, 1987; Wehner and Wehner, 1990). If a *Cataglyphis* forager encounters another one belonging to a different (conspecific) colony, this encounter usually does not lead to aggressive interactions. In ecological terms, scramble competition seems to be the way in which neighboring colonies compete with each other. Occasionally, however, real battles occur, engaging members of two colonies and leading to many injured and even dead ants. Furthermore, members of laboratory-reared colonies react very aggressively towards each other. What, then, are the parameters influencing aggressive behavior in this solitary forager?

In the present account we address the first question, whether the distance an individual ant has moved away from its nest correlates with this ant's state of aggressiveness. If this is the case, is aggressive behavior displayed in the context of defending the location of the colony rather than a food territory?

A second question we address is whether members of a colony are able to discriminate between members of yet unknown colonies and members of colonies with which they have had recent aggressive encounters. For resolving this question, we aimed to study the level of aggression between ants of two same colonies before and after encounters of individuals of these colonies. If such encounters leading to enhanced degrees of familiarity between the two colonies decreased or increased the level of aggressiveness between the members of the two colonies, learning some kind of an enemy specific template must have occurred and hence could be considered as an additional factor contributing to the "dear-enemy" phenomenon.

METHODS

Aggression Scores for Ants Captured at Different Distances from the Nest

We designed an experimental paradigm in which the degree of aggressiveness of individual ants taken from different colonies and captured at

different distances from their colonies (i.e., their nest entrances) could be recorded and quantified. In a small salt-pan area between Maharès and Chaffar (34.58°N, 10.50°E; Tunisia), 14 colonies were randomly divided into seven experimental pairs. Ants of these colonies were captured at distances of 0 m (experiment I), 1 m (experiment II), or 5 m (experiment III) from the nest entrance of one colony (colony A) and individually confronted with ants of another colony (colony B). The colony B ants were captured at a 20-m distance from their nest. All experiments were run in a reciprocal way (Fig. 1). In order to be able to discriminate individuals from different colonies during the confrontation tests, every ant was marked with a colony specific color dot applied to the gaster several hours before the tests started.

The ants were transferred to a Perspex box measuring 8 × 10 cm in ground area and 4.4 cm in height. The upper rim of the box was coated with Fluon to prevent the ants from escaping. An encounter within these boxes lasted 30 s. During an encounter, various states of aggressiveness were taken:

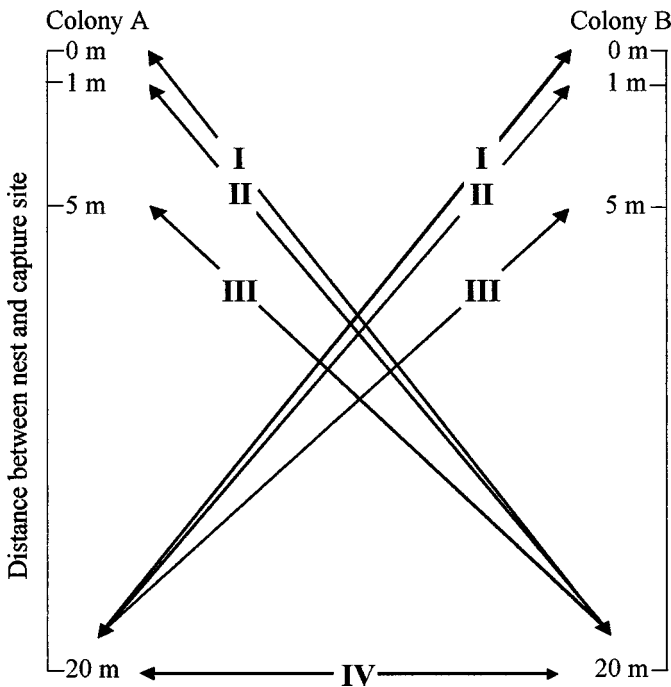


Fig. 1. Experimental paradigm: Ants captured at a 0-m (I), 1-m (II), 5-m (III), or 20-m (IV) distance from the nest entrance were individually confronted with conspecific ants belonging to another colony and captured at a 20-m distance from their nest.

(i) threatening with open mandibles, (ii) standing on top of the opponent, (iii) biting or twisting the gaster forward, and (iv) spraying formic acid were considered as being aggressive behaviors. The ant attacking first as judged by one of criteria *i* to *iv* was determined. The score was +1 when the "first attacker" was the ant captured closer to the nest, and it was -1 when the ant attacking first was captured 20 m away from its nest. Simultaneous aggression of both ants was scored 0. Encounters with no aggression were not scored but, nevertheless, were used in calculating the overall percentage of aggressive confrontations. The experiments were performed within the study area, but at least 20 m apart from either colony. After every encounter the Perspex boxes were cleaned with ethanol and dried for about 10 min in the sun. For each pair of colonies experiments I, II, and III were run 10 times, i.e., 5 times with ants of colony A captured closer to the nest and those of colony B captured farther from the nest, and 5 times, vice versa. The mean aggression scores of the 10 encounters were calculated. The results obtained from the seven colony pairs were tested against the zero hypothesis (no influence of distance from the nest on level of aggression) by applying two-sample *t*-tests. The overall percentages of aggressive confrontations for experiments I–III were compared by Friedman's multiple comparison test.

In experiment IV, three additional pairs of colonies were tested 10 times each. In this case both ants were captured at a 20-m distance from the nest. Therefore, aggression scores as defined above could not be determined, but the percentage of aggressive confrontations was recorded.

All tested ants were divided into four size classes, *s*, *m*, *l*, and *xl*, and confronted with ants of the same class. All experiments, I–IV, included confrontations with ants of the four size classes. We verified the classification in size classes by measuring head widths (at the level of the ventral borders of the compound eyes) of 80 additional size classified ants (*s*, 1.49 ± 0.10 mm; *m*, 1.72 ± 0.10 mm; *l*, 1.97 ± 0.12 mm; *xl*, 2.25 ± 0.08 mm; $N = 20$ ants for each size class; Kruskal–Wallis test for differences between size classes, $P < 0.001$).

Aggressiveness Toward Intruders of a Familiar Colony

Thirty colonies were randomly divided into 10 groups (each containing three colonies, A, B, and C). On the first day Test I was performed: ants of colony A were individually confronted with ants of the same size class (see above) of colonies B and C (Fig. 2). All ants were caught directly at the nest entrance. As previously described, during 30-s encounters within a Perspex box, the ant attacking first was determined. The behavioral response of the colony A ant was scored 0 when no aggression occurred, +1 when the A-ant

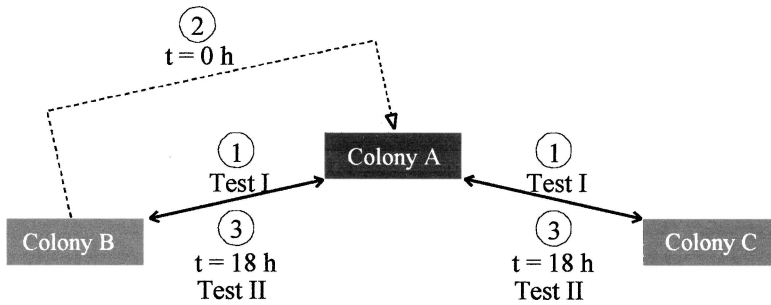


Fig. 2. Aggression tests between members of colony A and members of colonies B and C. The time course is denoted by ①, ②, ③. ① The preexperimental controls (Tests I) were performed; ② 15 colony B ants were introduced into colony A; ③ 18 h later, aggression tests (Tests II) were performed again between members of colony A and members of either colony B or colony C.

had threatened with open mandibles and/or stood on top of its opponent, and +2 when it attacked its opponent by biting or twisting its gaster forward and spraying formic acid. The same responses shown by ants of colonies B or C were scored 0, -1, and -2, respectively. The mean scores of 10 confrontations of A-ants with B-ants and 10 confrontations of A-ants with C-ants were computed. Once used in Test I, the experimental ants were not returned to their colonies to prevent reuse in Test II.

After these encounters had occurred, 15 new ants of colony B were experimentally introduced into colony A. Within less than 3 min all introduced ants were killed by members of colony A. Eighteen hours later Test II was performed, colony A ants were confronted either with colony B ants again or with colony C ants (Fig. 2). The mean scores recorded during Test I were subtracted from the scores measured in Test II.

The resulting values (scores I - scores II) were compared by applying the one-tailed Wilcoxon matched-pairs test.

RESULTS

Influence of the Ant's Distance from the Nest on the Ant's Level of Aggressiveness

The percentage of encounters leading to aggression decreased from experiment I (0-m vs. 20-m ants) to experiment III (5-m vs. 20-m ants; Table I; $P < 0.01$). If both ants were caught at large distances (20 m) from the nest (experiment IV), only 30% of the encounters ($N = 30$) led to aggressive

Table I. Effect of the Ant's Distance from the Nest on the Rate of Confrontations Leading to Aggressive Encounters^a

	Median [%]	Quartiles (25%, 75%)	Min., max. values	<i>P</i>
I	84	80, 88	75, 91] <0.05] <0.05] <0.01
II	76	69, 80	60, 84	
III	40	30, 45	20, 51	

^aFor experimental paradigms I, II, and III, see Fig. 1. $n = 7$ paired colonies with 10 aggressive encounters each. Statistics: Friedman's multiple comparison.

behavior, instead of 84, 74, and 37% in experiments I, II, and III, respectively (N in each case, 70).

In experiments I and II aggression was initiated more often by the ants captured closer to the nest than by the ones captured farther away from it (Table II; t -test, $P < 0.001$). This was not the case in experiment III (Table II; $P = 0.12$). The highest degree of aggression was observed in experiment I; the lowest, in experiment III. In conclusion, the level of aggressiveness displayed by an individual ant decreases with increasing distance from the nest.

Nevertheless, as mentioned above, even when both ants were caught at a 20-m distance from the nest, fights could be observed in 30% of the confrontations. As in this case, both ants were captured at identical distances from their nests, they should have exhibited the same level of aggression. Hence we must assume that 30% of aggressive encounters (corresponding to a probability of 0.3) resulted from three cases: (i) only ant a behaving aggressively, (ii) both ant a and ant b behaving aggressively, and (iii) only ant b behaving aggressively. Using the equations

$$0.3 = \text{pra} * (1 - \text{prb}) + \text{pra} * \text{prb} + (1 - \text{pra}) * \text{prb}$$

$$\text{case (i)} \quad + \quad \text{case (ii)} \quad + \quad \text{case (iii)}$$

and

$$\text{pra} = \text{prb}$$

Table II. Effect of the Ant's Distance from the Nest on the Degree of Aggression^a

	Median	Quartiles (25%, 75%)	Min., max. values	<i>P</i>
I	0.80	0.75, 0.99	0.72, 1.00] <0.05] <0.05] <0.01
II	0.70	0.59, 0.71	0.49, 0.81	
III	0.32	-0.03, 0.58	-0.23, 0.69	

^aScore +1 = aggressive behavior initiated always by the ants captured closer to the nest; score -1 = aggressive behavior never initiated by the ants captured closer to the nest; score 0 = aggressive behavior initiated by ants captured either closer to the nest or farther from it. $n = 7$ paired colonies, each with 10 aggressive encounters. Statistics: Friedman's multiple comparison.

with pra being the probability to fight for ant a and prb being the probability to fight for ant b , one can thus compute the probability for each 20-m ant to fight by

$$\begin{aligned}
 0.3 &= pra - pra^2 + pra^2 + pra - pra^2 \\
 \Leftrightarrow 0.3 &= 2 pra - pra^2 \quad | -1 | * (-1) \\
 \Leftrightarrow 0.7 &= (1 - 2 pra + pra^2) \\
 \Leftrightarrow 0.7 &= (1 - pra)^2 \quad |^{1/2} \\
 \Leftrightarrow 0.8367 &= 1 - pra \\
 \Leftrightarrow pra &= prb = 0.163
 \end{aligned}$$

as being 16.3%. Based on this value and the percentage of encounters leading to aggressive interactions in experiments I–III (see above), one can then calculate the probabilities to fight for ants caught at 0 m ($pr0$) with 84% aggressive encounters by

$$\begin{aligned}
 0.84 &= pr0 * (1 - 0.163) + pr0 * 0.163 + (1 - pr0) * 0.163 \\
 \Leftrightarrow 0.84 &= 0.837pr0 + 0.163pr0 + 0.163 - 0.163pr0 \\
 \Leftrightarrow 0.677 &= 0.837pr0 \\
 \Leftrightarrow pr0 &= 0.809
 \end{aligned}$$

as being 80.9%, that for 1-m ants (74% aggressive encounters) by

$$0.74 = prl * (1 - 0.163) + prl * 0.163 + (1 - prl) * 0.163$$

as being 68.9%, and that for 5-m ants (37% aggressive encounters) by

$$0.37 = pr0 * (1 - 0.163) + pr0 * 0.163 + (1 - pr0) * 0.163$$

as being 24.7%, respectively.

Can Colonies Be Primed Against Intruders from Another Colony?

Let us recall that ants of colony C were used as a control to decide whether the aggression of colony A ants toward members of colony B had really increased. Let us also recall that all specimens tested were taken directly from the nest entrance. The result was clear-cut: the level of aggression of colony A ants toward colony B ants increased significantly more than that of colony A ants toward control colony C ants (one-tailed Wilcoxon matched-pairs test, $P < 0.05$; Table III). In conclusion, the aggressiveness of ants belonging to a given society is higher toward members of colonies with which the given society has already had aggressive encounters.

Table III. Change of the Level of Aggression of Colony A Ants Against Colony B and Colony C Ants After the Insertion of Colony B Ants into Colony A^a

	Median	Quartiles (25%, 75%)	Min., max. values	<i>P</i>
A vs. B	0.30	0.05, 0.52	0.04, 0.6] <0.05
A vs. C	-0.18	-0.39, 0.20	-0.78, 0.81	

^aScore +2, high aggression initiated by colony A; score -2, high aggression initiated by colony B or C. *n* = 10 triplets of colonies A, B, and C were each tested 10 times, one against the other. The values reflect the difference between the experimental and the preexperimental scores (score Test I minus score Test II). Statistics: one-tailed Wilcoxon matched-pairs test.

DISCUSSION

Is the Ants' Aggressive Behavior Due to Nest Defense or Food-Territory Defense?

In *Cataglyphis fortis*, workers captured close to the nest entrance showed a higher level of aggression than those captured farther away from it. The percentage of encounters leading to aggression decreased from experiment I to experiment III (Table I). In contrast to the 0 and 1-m ants in experiments I and II, the 5-m ants in experiment III did not exhibit significant aggressive dominance (Table II). Hence, we expected almost no aggression to occur in experiment IV, in which both ants were caught 20 m apart from the nest. However, 30% of the encounters led to aggressive behavior, a value which enabled us to compute a probability of 16.3% that a 20-m ant would fight. In spite of this (low) fighting probability of 20-m ants, the steep decrease in the level of aggression from the 0-m ants to the 5-m ants is striking.

One explanation for the high levels of aggression at 0- and 1-m distances from the nest compared to the low levels at 5- and 20-m distances could be that some of the ants caught closer to the nest belonged to a soldier caste rather than to the forager force. A caste-dependent readiness to fight has been proposed in *Cataglyphis niger*, where largest individuals exhibit a higher level of aggression (Nowbahari *et al.*, 1999). However, we have excluded the effect of body size by performing tests with equally sized combatants. Furthermore, we have never observed any ants guarding the nest entrance. At the beginning and at the end of the daily foraging period, some ants occasionally get engaged in nest construction activities, but during the day, when the experiments were performed, all ants leaving the nest started to forage immediately. Therefore, it is unlikely that the different levels of aggression observed resulted from different worker cohorts. It is obviously the readiness to fight that decreases with increasing distance from the nest.

Hence, in *C. fortis* aggressive behavior seems to have evolved in the context of nest defense rather than food-territory defense.

Is Food-Territory Defense Useful for *C. fortis*?

Workers of *Cataglyphis fortis* forage individually for dead arthropods, a food randomly distributed (Wehner *et al.*, 1983) and therefore not easily monopolized. In addition, the large area searched by only about 50 workers per colony at any one time (Wehner, 1987) makes the defense of potential food territories almost impossible. Food territories have been found to occur in dominant ant genera containing species with numerous foragers such as wood ants, honeypot ants, weaver ants, and harvester ants (Hölldobler and Wilson, 1977; Hölldobler and Lumsden, 1980). According to a model proposed by the latter authors the cost/benefit ratio of territoriality depends not only on the richness of food provided by the territory, but also on the number of defending foragers and the size of the defended area. For example, small colonies such as those of *Leptothorax* species, consisting of only a few dozen workers, focus their aggression mainly on nest defense (Heinze *et al.*, 1996), while large colonies as in *Pogonomyrmex* defend not only the closer nest vicinity, but also the trunk trails (Hölldobler, 1976). According to this model territorial behavior would not be expected in *C. fortis*, which—similarly to *Leptothorax*—has rather small colonies but, in addition, extensive foraging areas.

What Is the Cue Eliciting Nest Defense in *C. fortis*?

Sakata and Katayama (2001) report that in the nest defense of *Lasius niger* the level of aggression of any ant increases when at least 20 nestmates are around. In fact, the presence of concolonial mates raised an individual's readiness to defend such places. In *Cataglyphis niger* (Wenseleers *et al.*, 2002), *C. cursor* (Mayade *et al.*, 1993), and several *Tetramorium* species (Cammaerts and Cammaerts, 2000), the level of aggression is raised by odor cues rather than by the presence of ants per se. Ants of these species mark the vicinity of the nest with pheromones and attack nonnestmates more frequently when these odors are present. As for *C. fortis* the forager force is small, it is difficult to use the number of nestmates as a recognition cue for the vicinity of the nest. Furthermore, due to the high surface temperatures prevailing in the *C. fortis* habitat, marking the nest vicinity by pheromones might not be an effective strategy. Consequently the cue eliciting defensive behavior in *C. fortis* might be the individual ant's perceived vicinity to the nest.

How Does an Ant Assess Its Distance from the Nest?

An ant could do so on the basis of the time elapsed since it has departed from the nest. Given a mean walking speed of $16\text{--}40\text{ cm} \cdot \text{s}^{-1}$ (Ronacher and Wehner 1995), a *C. fortis* worker having left the nest should reach a 5-m distance from the nest within much less than a minute. However, in our experiments 5 to 10 min had passed before the ants captured at the nest entrance were tested in our aggression paradigm. Most likely it is the ant's continually running path integration system (see, e.g., Müller and Wehner, 1988) that informs the animal about its distance from the nest. By using this system, *C. fortis* should be able to adjust its level of aggression precisely without the aid of nest-related external cues.

Is the Vicinity of the Nest the Only Parameter Affecting a Forager's Level of Aggressiveness?

Occasionally, when *C. fortis* ants had been trained to visit an artificial feeder (pieces of watermelon), individual ants were observed to stay at the feeder for extended periods of time. They then reacted highly aggressively to every arriving conspecific nonnestmate. This occurred even if the feeder was 15 m away from the nest entrance. Although stable patch-like food sources do rarely exist in the habitat of *C. fortis*, the ants seem to be able to raise their level of aggressiveness if such food sources occur suddenly. In *Lasius niger*, such an increase in food site-related aggressiveness, again, depends on the presence of numerous nestmates (Sakata and Katayama, 2001). We do not yet know whether or not this applies to *C. fortis* as well. In this context, however, one observation made by Sibylle Wehner on July 9, 2002, is worth mentioning. An individual *C. fortis* forager, being the only one at a feeder 15 m apart from the nest entrance of the experimental colony, successfully attacked any conspecific ant arriving at the feeder from another colony (located at a 22-m distance from the feeder). The attacking ant was grasping the "intruders" at their mandibles, biting them at their alitrunk, and even dragging them by their legs away from the feeder for a few centimeters. It may well be that the feeder-defending ants use the same system as the nest-defending ones to adjust their level of aggression in relation to their distance from the feeder. Nevertheless, we could not find any evidence for the existence of stable food territories. This negative result is in accord with the model provided by Hölldobler and Lumsden (1980) and predicting that only colonies with a large ratio of forager force to foraging area should invest in the defense of stable territories.

Having shown that an individual ant's level of aggression is not stable but adjustable we posed the following question.

Can a Colony Get Primed Against Intruders from a "Known" Foreign Colony?

During five 3-month summer observation periods we found only one natural case of an escalated fight between two colonies, with 20 workers involved and resulting in 12 killed ants. There was no food source around, no nest entrance nearby, and no other conspicuous cue or object worth competing for which could explain this costly event for both combative groups.

Given the costs of aggressive behavior it is pertinent to ask whether colonies which have been in conflict in the past act more aggressively toward each other than they do toward unknown colonies. Indeed, in experiment 2, when alien conspecific ants were intruded into a colony, this colony's ants increased aggressiveness toward members of the intruder colony but not toward members of a conspecific control colony. Hence, the workers of the focus colony were able to discriminate not only between nestmates and nonnestmates, but also between unknown alien workers and workers of a colony with which they had experienced a previous encounter.

This increase in aggression against familiar, conspecific nonnestmates is at variance with the widespread "dear-enemy" phenomenon (Getty, 1987, 1989; Ydenberg *et al.*, 1988). In ants this phenomenon was found in *Pheidole tucsonica* and *P. gilvescens* (Langen *et al.*, 2000) as well as in *Leptothorax nylanderi* (Heinze *et al.*, 1996). Habituation and environment-based as well as genetic cues have been identified as proximate causes for graded levels of aggression toward conspecifics (habituation [Langen *et al.*, 2000], environment-based cues [Heinze *et al.*, 1996], genetic cues [Beye *et al.*, 1998; Pirk *et al.*, 2001]). The functional significance of the dear-enemy phenomenon is a better assessment of the motivation and fighting ability of familiar neighbors. In his extensive review Temeles (1994) points at the different threats caused by the usurpation of the territory or the nest by strangers and neighbors.

In *C. fortis* the situation cannot be explained by habituation, because the response toward familiar nonnestmates was even more aggressive than it was against unfamiliar nonnestmates. Also, environment-based cues and a correlation of genetic and geographic distances cannot account for the increased aggression of *C. fortis* ants toward conspecifics, because we tested the very same colonies before and after they had been in conflict with each other. Most likely the ants rely on an "enemy-specific" template as has also been

shown for *Pheidole* ants, which focus their alarm-recruitment force mainly on their most dangerous enemies, ants of the genus *Solenopsis* (Wilson, 1975, 1976; Feener, 1986). This behavior may have evolved in response to long-standing ecological pressures exerted by this fire-ant enemy, but it can be experimentally extended to other species as well (Carlin and Johnston, 1984). Colony-specific enemy recognition has also been shown for *Pogonomyrmex barbatus*, in which the foraging activity is more disturbed by conspecific neighbors than by conspecific strangers. This might be due to neighboring colonies posing a major threat to the food territory of a colony (Gordon 1989).

In principle, there are at least two proximate factors that could be responsible for recognizing familiar neighbors. (i) Environmental cues are known to affect the colony odor (Obin, 1986; Heinze *et al.*, 1996). By comparing the “environmental” part of a nonnestmate’s label, ants might be able to distinguish conspecific neighbors from conspecific strangers. (ii) Ants are known to adjust their internal olfactory template to changing colony odors (Obin, 1986; Errard and Hefetz, 1997). This flexibility might enable them to learn a second—in the present case, enemy-specific—template. In *C. fortis* the first hypothesis can be ruled out. In contrast to the experiments performed in *Pogonomyrmex barbatus* (Gordon, 1989), the *Cataglyphis* ants studied in the present account did not have to discriminate between nearby colonies and colonies from afar. The only difference between the “unknown” and the “known” colonies was the artificial introduction of a small number of (15) ants of the latter colony to the focus colony. Thus, the *C. fortis* workers must have learned a second, enemy-specific, olfactory template. By comparing another ant’s label with a set of at least two different templates, an ant could respond socially positively when the label fits the “colony template,” socially negatively when it fits the “enemy template,” and neutrally when it does not fit either template. These discrimination, learning, and retrieval capacities would enable *C. fortis* to focus its costly aggressive endeavors on colonies which, due to past experience, pose a real threat. Red harvester ants are able to discriminate conspecific workers of different tasks just by their hydrocarbon profile (Greene and Gordon, 2003), which needs a more complex system than a simple matching of another ant’s odor with the colony-specific odor. The existence of a learned enemy-specific template in *C. fortis* is further proof of discriminatory power in ants. Nevertheless, apart from these colony-specific responses there is also an increased readiness to fight against “unknown” conspecifics whenever the “defender” is close to its nest entrance (see experiment I). In conclusion, the decision whether or not to fight is based on the concerted action of a general (distance to nest-dependent) internal state of aggressiveness and a particular olfactory matching-to-template process.

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